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## Selected Features of the Desmostylian Skeleton and Their Phylogenetic Implications

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### ABSTRACT

According to several standard descriptions, desmostylians lack certain specializations shared by proboscideans, sirenians, and hyracoids. These specializations are amastoidy and the serial arrangement of the carpals with the concomitant loss of contact between the lunar and unciform. We argue that original descriptions of desmostylians

pertaining to these traits are either in error, or have alternative phylogenetic implications. Hence, comparisons of these conditions do not exclude desmostylians from the superordinal group Tethytheria (proboscideans and sirenians) or the more inclusive Paenungulata (tethytheres and hyracoids).

### INTRODUCTION

The Desmostylia are an extinct order of mammals with specializations of the skeleton suitable for an amphibious mode of life. Although this group was formerly associated with the aquatic Sirenia (Simpson, 1945), and is now placed within a superordinal category Tethytheria, which also includes the Proboscidea and Sirenia (McKenna, 1975), these avowed relationships present some problems. According to standard descriptions, desmostylians lack certain skeletal specializations shared by Proboscidea and Sirenia. Specifically, desmostylians were claimed to

be more conservative than sirenians (and, by implication, proboscideans) with respect to the reduction of mastoid exposure (Hay, 1915; Abel, 1922; VanderHoof, 1937) and the serial arrangement of the carpal elements (Shikama, 1966). These differences have influenced more recent students of the problem (e.g., Tassy, 1981), who have opted for a close association of Proboscidea (including the late Eocene–early Oligocene genus *Moeritherium*) and Sirenia to the exclusion of Desmostylia.

Of significance is the fact that the above

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cited specializations, though supposedly lacking in desmostylians, are found in hyracoids as well as proboscideans and sirenians. Such features have been used as evidence for the monophyly of the Paenungulata, a superordinal group comprising tethytheres and hyracoids (Gregory, 1910; Shoshani et al., 1978; Novacek, 1982, 1986). Hence, the lack of certain apomorphies in desmostylians not only presents a difficulty for recognition of the Tethytheria but also for the more inclusive Paenungulata, if Desmostylia are to be retained within these groups.

Here we offer arguments why published descriptions of desmostylians with respect to the characters in question are either incorrect, or are subject to alternative phylogenetic interpretations. Our emendations allow assignment of the Desmostylia to the Tethytheria. They are also consistent with a paenungulate grouping for tethytheres and hyracoids.

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#### CHARACTER ANALYSIS

Desmostylians include the nominal genera *Desmostylus*, *Paleoparadoxia*, *Cornwallius*, *Vanderhoofius*, *Kronokotherium*, and *Behemotops* (Hay, 1915; VanderHoof, 1937; Pronina, 1957; Reinhart, 1959; Ijiri and Kamei, 1961; Shikama, 1966; Domning et al., 1986; *Kronokotherium* and *Vanderhoofius* may be junior synonyms of *Desmostylus*, D. Domning, personal commun.). Of these, only *Desmostylus* and *Paleoparadoxia* are well represented by nearly complete skulls and skeletons, and even in such cases damage during preservation has contributed to some

of the ambiguities discussed below. The characters below are of note.

#### MASTOID EXPOSURE

Typically (and primitively) within mammals the mastoid portion of the petrosal is well exposed on the exterior surface of the skull, as it forms a broad flange in the occiput lateral to the exoccipital and medial and posterior to the squamosal (Novacek and Wyss, 1986). However, the mastoid is not exposed in this fashion in the occiput of certain mammals, including pholidotans, cetaceans, dermopterans, advanced artiodactyls, proboscideans, sirenians, and hyracoids. This, the "amastoid condition" is clearly derived for mammals (Novacek and Wyss, 1986).

Sirenians show exposure of the mastoid via a large fenestra in the dorsal occiput, but this seems a uniquely specialized condition. Although the mastoid is inflated and essentially fills this large fenestra, it does not extend around the base of the cranium to form a flange on the ventral occiput. Thus, sirenians do not show the continuous mastoid exposure between the horizontal basicranium and ventral (vertical) occiput that is characteristic of most mammals. The opening of the occipital fenestra for dorsal exposure of the inflated mastoid is therefore likely a secondary feature, and one that could well derive from the amastoid condition exemplified by hyracoids and proboscideans.

The broad occipital exposure of the desmostylian mastoid was explicitly described by Hay (1915, p. 387), figured but not described by Abel (1922, fig. 3), and figured and discussed by VanderHoof (1937, figs. 11, 12). These descriptions are based on a skull of *Desmostylus hesperus* (USNM 8191). VanderHoof's (1937) figure 12 of this specimen shows a mastoid element only on the left side of the skull. Although he did not label sutures, it appears from his figure 12 that the mastoid on the left side of the skull is isolated on its lateral border by a short, curved suture and on its medial border by a long, vertically oriented suture that runs to the lambdoidal rim (fig. 1A herein). However, the "lateral suture" is more likely a contact between the occipital exposure of the squamosal and the

exoccipital (fig. 1B). Contrary to VanderHoof's figure, this suture runs all the way to the occipital foramen. The suture is also preserved on the right side of the skull where it appears to extend beyond the occipital foramen and join the oblique supraoccipital-exoccipital suture either at the lambdoidal crest or at a somewhat more medial junction (fig. 1B). The "medial suture," which VanderHoof (1937) and others seem to have taken as the mastoid-exoccipital suture, is an artifact, a crack in the bone. It is clearly not present on the right side of USNM 8191. It crosses, rather than joins, the "lateral suture" (cf. fig. 1A, 1B). It trends lateral to the occipital foramen; this foramen typically lies within the mastoid or exoccipital or in a suture separating these elements from the supraoccipital. The "medial suture" also marks the lateral edge of a damaged area where surface bone has been removed.

We conclude, then, that earlier descriptions of this important specimen are in error and there is clearly no exposure of the mastoid on the occiput in *Desmostylus hesperus*. Moreover, published figures and descriptions of *Desmostylus hesperus japonicus* (a senior synonym of *Desmostylus mirabilis* Nagao, Ijiri and Kamei, see Shikama, 1966) and *Pa-leoparadoxia tabatai* (Ijiri and Kamei, 1961, pl. 1, fig. 4 and pl. 3, fig. 5) do not indicate a mastoid in the occiput. Instead, these figures correspond closely with the geometry of elements reconstructed in figure 1B. Finally, immature specimens (USNM 181744) of *Desmostylus hesperus* (fig. 2) and *Cornwallius* sp. (USNM 181788) show neither mastoid exposure nor VanderHoof's (1937) "medial suture" in the occiput.

The broad invasion of the squamosal on the occipital surface in *Desmostylus* (figs. 1B, 2) is a curious feature. This arrangement, however, bears striking resemblance to that in Sirenia where the occipital exposure of the squamosal is even more marked. It is clear, then, that the ventral mastoid is concealed in these taxa by the expansive paroccipital apophysis formed by broad contact between the squamosal and exoccipital. Only in sirenians does a large fenestra expose, more dorsally, the inflated mastoid process. As noted above, we regard this fenestra as a high-

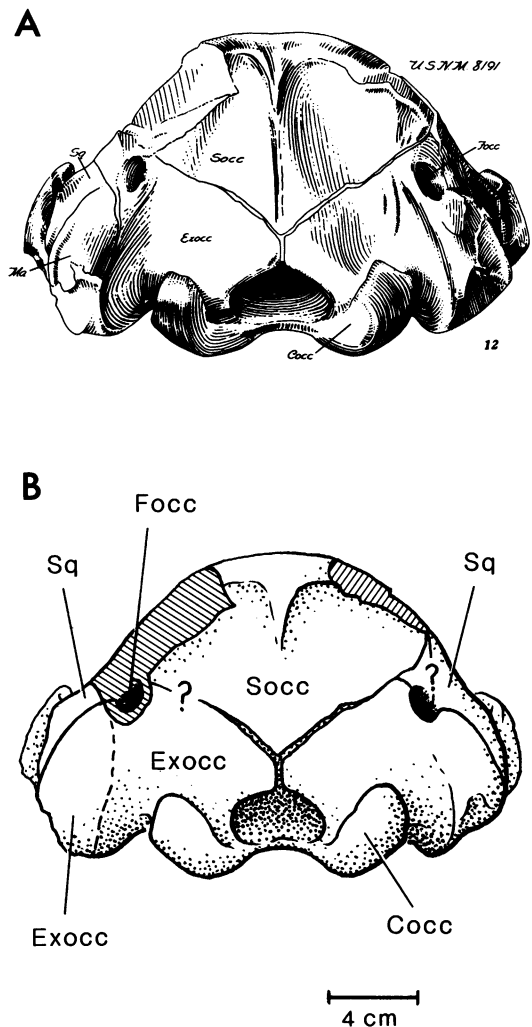


Fig. 1. Posterior views of occipital region in USNM 8191, *Desmostylus hesperus*. (A) Reconstruction from VanderHoof (1937, fig. 12). (B) Reconstruction favored in this paper. Symbols are Exocc, exoccipital; Focc, occipital foramen; Ma, mastoid process (of the petromastoid); Cocc, occipital condyle; Socc, supraoccipital; Sq, squamosal. Dashed line indicates crack in the bone surface. Hatching indicates damaged area.

ly derived feature. It probably represents the marked expansion of the occipital foramen, which in *Desmostylus* is also atypically large (figs. 1A, 1B, 2). The amastoid condition noted for tethytheres and hyracoids is thus attained in desmostylians.

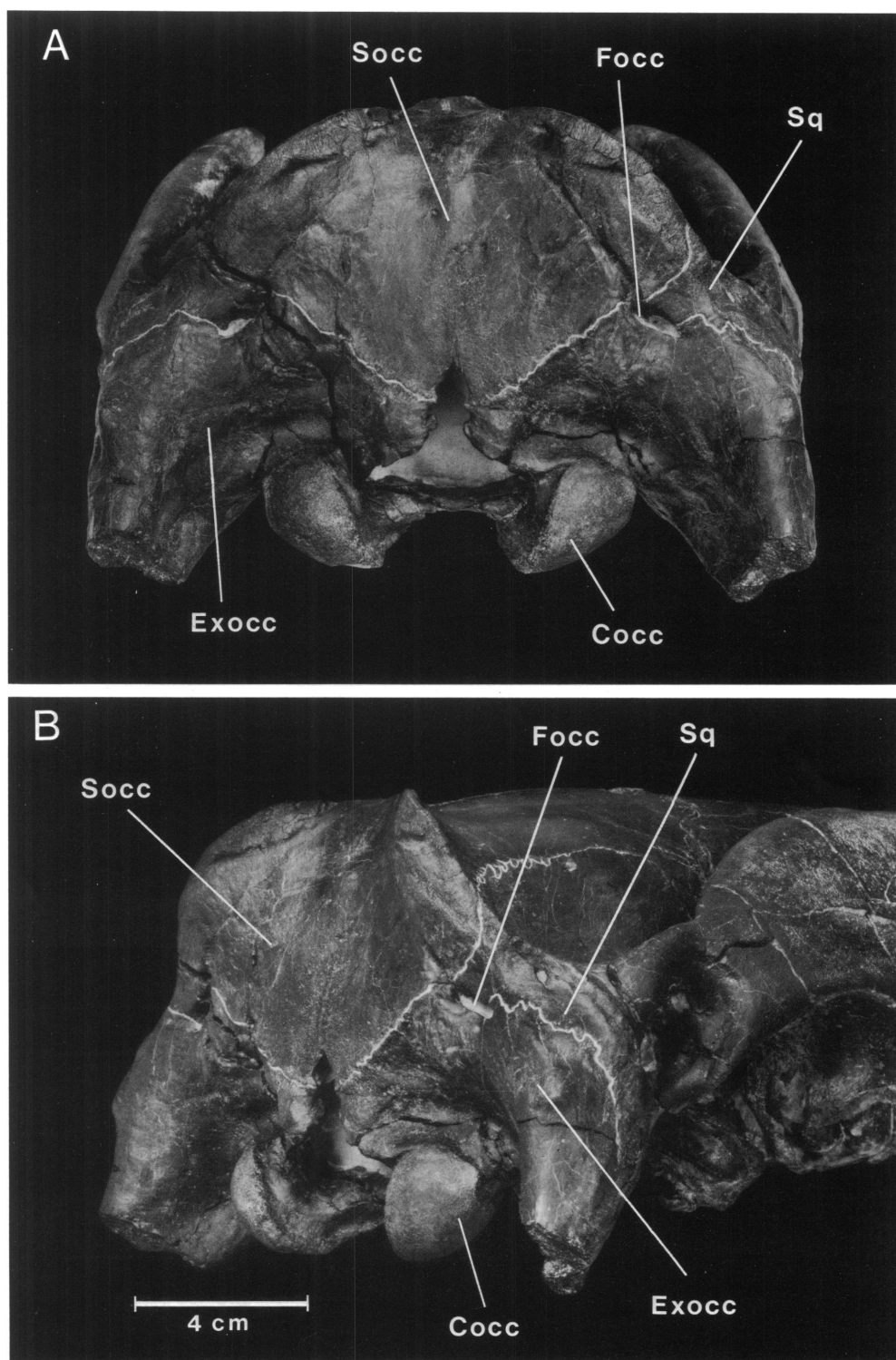


Fig. 2. Posterior view of the occipital region in USNM 181744, immature skull of *Desmostylus* cf. *hesperus*. Abbreviations defined under fig. 1. Note that sutures were not painted, but merely cleaned.

## CARPAL ARRANGEMENT

A general condition in many amniote groups is the alternating arrangement between the proximal and more distal carpal elements. This arrangement allows an oblique contact between several elements, including the lunar and unciform. The alternating condition is characteristic of therapsids, monotremes, marsupials, edentates, rodents, insectivores, creodonts, carnivores, pantodonts, tillodonts, primates, various condylarths, notoungulates, tubulidentates (fide Shikama, 1966, but contra Gregory, 1910), perissodactyls, and artiodactyls (see survey in Gregory, 1910).

A more derived condition is represented by a serial arrangement of the carpals, wherein the proximal and distal elements do not strongly overlap, and oblique contact between these elements, including the lunar and unciform, is lost. Although the serial arrangement is found in a few extinct lineages (e.g., phenacodontid condylarths, some litopterns) the distribution of this specialized condition at a higher level is notably restricted. The only mammalian orders that can be characterized by this feature are the Hyracoidea, Proboscidea, Sirenia (contra Gregory, 1910), Cetacea, and the extinct Embrithopoda. (It is likely that embrithopods have a special relationship to proboscideans, sirenians, and hyracoids—see McKenna, 1975, p. 42.) Of these orders, the cetacean condition, at least, clearly seems an independent derivation. The putative relatives of the cetaceans, the mesonychids (Van Valen, 1966; McKenna, 1975) have alternating carpals and retain the lunar-unciform contact. This is, then, the most plausible condition for the ancestor of whales and their nearest sister taxon.

Because of its limited distribution, the serial carpal arrangement of sirenians, proboscideans, and hyracoids represents a potential synapomorphy for Paenungulata (Shoshani et al., 1978; Novacek, 1982). However, desmostylians are claimed to retain the more conservative alternating pattern and a strong, overlapping contact between the lunar and unciform (Shikama, 1966, p. 139, fig. 108). This contradiction poses a major difficulty for allocation of desmostylians to the paenungulates.

We believe that the putative alternating pattern of the carpals in desmostylians is either questionable or a highly specialized arrangement that is clearly not equivalent to the primitive condition for mammals. The critical material to consider here is the postcranial skeleton of the best represented taxon, *Paleoparadoxia tabatai*. Despite Shikama's (1966, fig. 108; 1968, pl. 4; and fig. 3A herein) astute analysis of this material, he had to contend with certain ambiguities, due to distortion of elements in the preserved specimens. The bones of the carpus in the Izumi specimen of *Paleoparadoxia* are not closely imbricated and there are alternative interpretations of their natural arrangement (Shikama, 1966, pp. 34–38). Shikama (1966, fig. 15) claimed that the lunar (bone 34 in his fig. 15) in the Izumi specimen makes a distolateral contact with the unciform (bone 36). This is an odd contact because the overlap of these elements in the Izumi specimen lies along an oblique, proximal-distal axis rather than the mediolateral axis characteristic of the alternating arrangement (fig. 3B). It is noteworthy that, except for the lunar, the proximal carpals do not strongly overlap in contact with the distal carpals (Shikama, 1966, pp. 135–138; and fig. 3A herein).

The cuneiform and unciform are basically aligned, although the lunar intrudes to contact the medial facet of the latter element. The lunar is enlarged in a peculiar fashion to the extent that it nearly contacts metacarpal III (fig. 3A). Also the trapezoid lies distal to the scaphoid, but it does not make close contact with more central proximal elements (the lunar or the centrale), as it does in figure 3B. In fact, the relationship of the scaphoid-lunar-trapezoid-magnum quartet in *Paleoparadoxia* is more reminiscent of that in sirenians (fig. 3C) than in the primitive mammals (fig. 3B).

Shikama (1966, p. 139) stressed that the desmostylian carpal arrangement differs from the usual conditions where a lunar-unciform contact is present. For example, in Perissodactyla and Artiodactyla, there is an intimate contact between the scaphoid and magnum not seen in desmostylians. Moreover, Shikama (ibid.) noted that the proximodistally compressed scaphoid, cuneiform, and "platy" unciform in desmostylians suggested a pos-

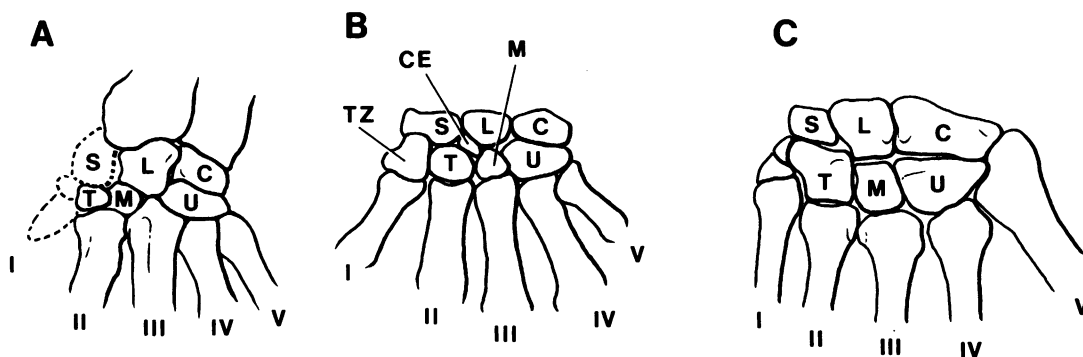


Fig. 3. Left manus of (A) *Paleoparadoxia tabatai* (after Shikama, 1966, figs. 15, 17, 18, 108; 1968, pl. 4); (B) *Pantolambda bathmodon* (American Museum of Natural History [AMNH 2546] after Matthew, 1937, fig. 42, p. 180) and (C) *Trichechus* sp. (American Museum of Natural History, Comparative Anatomy Collections [AMNH-CA 30]). Symbols are C, cuneiform; CE, centrale; L, lunar; M, magnum; S, scaphoid; T, trapezoid; TZ, trapezium; U, unciform. Not to scale. (B) is taken to represent a generalized condition for eutherians, although the centrale has been lost in many lineages. Note that in (B) the lunar-unciform contact lies along the mediolateral axis separating the proximal and distal carpal elements. Overlap in (A) is largely effected by the distal enlargement of the lunar.

sible relationship with Proboscidea and Embrithopoda. Our examination of a cast of the Stanford skeleton of *Paleoparadoxia* corroborates the above assessment of the material described by Shikama. (This specimen, *Paleoparadoxia*, University of California Museum of Paleontology (UCMP) 81302, was discovered in 1965, but has never been formally described.)

It is difficult to assess the phylogenetic implications of these comparisons. The question of transformation of the mammalian carpus is in need of modern treatment. Nevertheless, the desmostylian condition seems to us an anomalous one in several respects, and the condition might be considered a potential autapomorphy for the group. Assuming that the lunar-unciform contact in *Paleoparadoxia* is properly reconstructed, this articulation is effected by a distally expanded lunar element that nearly contacts metacarpal III. It is conceivable that this unique system derived from a more basic serial carpal arrangement. At the very least, the desmostylian condition is not comparable to the typical alternating pattern in mammals (cf. fig. 3A, 3B).

#### PHYLOGENETIC INTERPRETATIONS

The specialized amastoid condition noted above is shared by hyracoids, desmostylians, proboscideans, and sirenians. It thus helps to

characterize a grouping at a higher level than those for which it has often been applied. Tassy (1981, fig. 12) argued that the reduction of the mastoid apophysis was a synapomorphy uniting proboscideans with sirenians and excluding desmostylians. He retained desmostylians within the tethytheres, citing the following characters as synapomorphies for the group; (1) forward placement of the orbit, (2) position of the infraorbital foramen directly below the orbit (obviously correlated with character 1), (3) the strong zygomatic process formed by the laterally directed squamosal, and (4) the bilophodont-bunolophodont molars. Tassy (1981) noted a problem with the remote position of desmostylians, because he thought this fossil group showed some special similarity to sirenians (see Tassy, 1981, fig. 12, characters 14, 25, and discussion therein) that did not apply to proboscideans. He was left with two mutually contradictory groupings—one favoring a closest relationship between sirenians and desmostylians on the basis of the above cited characters, and one favoring a closest relationship between proboscideans and sirenians on the basis of the amastoid condition. Since, as we argue, amastoidy is also common to desmostylians, this contradiction is eliminated. Clearly, amastoidy is not useful for defining tethytheres (including desmostylians) because the character is common to hy-

racoids. The trait does seem a potentially useful synapomorphy for Paenungulata if it can be argued that amastoidy in a few other mammalian lineages (pholidotans, dermopterans, advanced artiodactyls) was independently derived (Novacek and Wyss, 1986).

There is little doubt that the serial carpal arrangement also describes a more inclusive group than Tethytheria. The arrangement in hyracoids is closely similar to that in tethytheres (Shikama, 1966) and the condition seems a potentially useful synapomorphy for Paenungulata (Shoshani et al., 1978; Novacek, 1982, 1986; Novacek and Wyss, 1986). Desmostylians still pose a problem for this generalization. Here we maintain that the reconstruction of the alternating carpal arrangement in desmostylians is either (1) open to question or (2) the result of a uniquely specialized pattern involving the hypertrophy of the lunar element. Thus the carpal evidence does not unambiguously preclude the allocation of desmostylians to Paenungulata.

In closing we note that this paper addresses directly only the validity of certain characters attributed to desmostylians and the implication that such characters would exclude desmostylians from either Tethytheria or Paenungulata. We have elsewhere (Novacek and Wyss, 1986) favored the inclusion of desmostylians within Tethytheria on the basis of additional characters cited by Tassy (1981) and others. Left open is the question of desmostylian relationships within Tethytheria. We do not argue here whether desmostylians are the closest relatives of sirenians or proboscideans or are the most remote of the tethythere clades.

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